

Responses of four Critical Weight Range (CWR) marsupials to the odours of native and introduced predators

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ABSTRACT

In Australia many critical weight range (CWR) species are threatened by predation from the introduced Red Fox *Vulpes vulpes*. Understanding how these prey species respond to native predators such as the Tiger Quoll *Dasyurus maculatus*, and comparing their responses to foxes is important in understanding why fox predation is such a problem. Many northern hemisphere mammalian species have developed responses to the odours of the main species which prey upon them. The situation in Australia remains unclear. We looked at the effect of scenting traps with the faeces of the Tiger Quoll and the Red Fox on the capture rates of four species of CWR marsupials, the Long-nosed Bandicoot *Perameles nasuta*, the Southern Brown Bandicoot *Isodon obesulus*, the Northern Brown Bandicoot *I. macrourus* and the Common Brushtail Possum *Trichosurus vulpecula*. None of these species responded to fox odour. However despite low capture rates, Northern Brown Bandicoots and Common Brushtail Possums were captured significantly more often in traps scented with Tiger Quoll faeces. This indicates that these species may be responding to predator odours, but not with the traditionally expected avoidance. Reasons for why this may be so are discussed.

Key words: predator/prey interactions, scat, chemical signal exploitation, fox, quoll, possum, bandicoot.

Introduction

In the past 200 years 16 species of mammals have become extinct in Australia, representing 50% of the total world mammalian extinctions over that time period. (Short and Smith 1994). All of these extinctions have been species whose body mass lie within what has become termed the Critical Weight Range (CWR) of 35g to 5500g (Burbidge and McKenzie 1989). Habitat loss, changes to fire regimes and competition have been proposed as possible causative agents. But predation by the Red Fox *Vulpes vulpes* which was successfully introduced to Australia in the 1870s (Rolls 1969), has been identified as a primary cause of the decline or extinction of 35 species which fall within the CWR (Burbidge and McKenzie 1989). The CWR coincides with the preferred prey-size range of the Red Fox (Henry 1996; Smith and Quin 1996), and the spread of the fox coincided with many recorded extinction events (Mahon 2001). It has been suggested that CWR species high daily metabolic requirements and/or low mobility may leave them more vulnerable to predation (Burbidge and McKenzie 1989; Morton 1990). However, prior to the introduction of the fox, these CWR mammals were prey for native marsupial predators, such as the Tiger Quoll *Dasyurus maculatus* (also widely known as the Spotted-tailed Quoll), to which they would have been just as vulnerable. So it is unclear why these CWR prey were seemingly so vulnerable to predation by introduced Red Foxes.

Where predator and prey have co-evolved, natural selection has frequently led to an 'arms race' in detection and concealment strategies amongst enemies (Dawkins and Krebs 1979). In particular, eavesdropping on predator signals has become a key weapon by which prey may estimate their predation risk. For example, many northern hemisphere mammalian species avoid the odour of their major mammalian predators (Stoddart 1976; Dickman and Doncaster 1984; Gorman 1984; Calder and Gorman 1991). By avoiding areas contaminated with these odours they are thought to reduce the likelihood of encountering predators, and increase their chances of survival. In Australia, native prey species have evolved with Tiger Quolls over millions of years, but foxes have only been present in Australia for the past 130 years (Rolls 1969; Mahon 2001). Indeed, Australia's mammalian fauna has evolved in relative isolation for around 40 million years, and is dominated by marsupials, rather than placental mammals as throughout the rest of the world (Strahan 1998). Thus potential prey may have defences which have evolved mechanisms to reduce predation by marsupials such as Tiger Quolls, but these may not function for evolutionary novel predators like foxes (Russell *et al.* 2003). Similarly, defences which have evolved to reduce predation by foxes among northern hemisphere prey species may not have evolved

in Australia at all. Moreover, predator odour recognition may not necessarily have evolved in the same way as the rest of the world.

Evidence for the role of phylogeny or co-evolutionary history in the exploitation of odours in mammalian predator-prey interaction is currently lacking. It is not known whether marsupials avoid odours from either marsupial or placental predators and there is equivocal evidence in assessing whether placental prey species respond to marsupial predator odours or if co-evolution matters. Introduced House Mice *Mus domesticus* avoid the faecal odour of the Red Fox, the Feral Cat *Felis catus*, and to a lesser degree the native Western Quoll *D. geoffroyi* (Dickman 1992). However, Banks (1998) reported no aversion by two native species, the Bush Rat *Rattus fuscipes* and the Agile Antechinus *Antechinus agilis*, to the faeces of the Red Fox. Similarly Banks *et al.* (2003) found that Domestic Dog *Canis lupus familiaris* faeces at traps did not alter the capture rate of Bush Rats. Aversion to domestic dog urine has been reported for Swamp Wallabies *Wallabia bicolor* (Montague *et al.* 1990) and to synthetic predator odours for Common Brushtail Possums *Trichosurus vulpecula* (Woolhouse and Morgan 1995; Morgan and Woolhouse 1997), however in both cases this was determined by the consumption of seedlings that had been sprayed with the odour source, and this aversion may have been due to taste rather than odour. Blumstein *et al.* (2002) found that the feeding choices of Tammar Wallabies *Macropus eugenii* and Red-necked Pademelons *Thylogale thetis* were not affected by Red Fox, Kodiak Bear *Ursus arctos* and Dingo *C. lupus dingo* faeces or Domestic Dog urine, although Gresser (1996) did find that a combination of Red Fox urine and faeces decreased the amount of food eaten by Common Brushtail Possums.

In this paper we use a replicated field experiment to test whether four CWR marsupials, the Long-nosed Bandicoot *Perameles nasuta*, the Southern Brown Bandicoot *Isodon obesulus*, the Northern Brown Bandicoot *I. macrourus* and the Common Brushtail Possum avoid odour cues from a native marsupial predator, the Tiger Quoll or an introduced placental predator, the Red Fox. Each species is preyed upon by both quolls and foxes (Alexander 1980; McKay 1994; Belcher 1995; Jones and Barmuta 1998), and all four species use scent-marking for intra-specific communication (Stoddart 1980; Gordon 1998; Scott *et al.* 1999; Kerle 2001), indicating well developed olfactory abilities to support potential recognition of predators. We use the scat at trap technique used in many northern hemisphere studies to demonstrate odour avoidance by potential prey. If these CWR mammals recognise and avoid predator odours as a predation risk, we predict that traps with faeces should have lower success than untreated traps.

Method

Long-nosed Bandicoots and Common Brushtail Possums were trapped at the end of August in Sydney Harbour National Park in Sydney, Latitude 33° 48' S Longitude 151° 17' E, at the boundary of thick heath and the open grassy areas around the old quarantine station located in the park. Tiger Quolls are not found in the National

Park (Skelton *et al.* 2003), while Red Foxes enter every five years or so, killing large numbers of wildlife before being removed by park staff (Banks 2004). Cage traps (50 x 19 x 19cm), baited with bread and peanut butter and enclosed in green shade cloth to provide protection from the elements, were set in four transects lines, each consisting of six trap stations, for three consecutive nights on two separate occasions, with different transects being utilised on each occasion. Southern Brown Bandicoots and Northern Brown Bandicoots were trapped during early September using large aluminium live-capture Elliott traps (46 x 16 x 16cm), baited with a mixture of rolled oats, peanut butter and vegetable oil, and set out in a grid of 15 trap stations (3 x 5). Northern Brown Bandicoots were trapped in wet and dry heath in Myall Lakes National Park (latitude 32° 28' S, longitude 152° 24' E), three hours north of Sydney. Southern Brown Bandicoots were trapped in heath and open woodland in Garigal National Park (33° 43' S, 151° 11' E) in Sydney's north. Both Tiger Quolls and Red Foxes are known to be present in both Myall Lakes (McKay 1994) and Garigal (NSW National Parks and Wildlife Service 1998) National Parks. For these bandicoot species, trapping took place over three consecutive nights, and three grids were trapped on separate occasions. Whenever an animal was caught, the trap was removed and replaced with a fresh clean trap.

For all species, trap stations comprised three traps placed one metre apart in a star formation, with stations 25-30 metres apart. At each station, one trap was scented with fox scat, one trap with quoll scat, and one trap was left untreated. This technique has been used extensively before to examine the issue of predator avoidance (Stoddart 1976; Calder and Gorman 1991; Dickman 1992; Banks 1998) and both (Banks 1998) and our recent work on small mammals (Russell and Banks unpublished data) found no difference between the results of this technique and placing a single trap (either scented or unscented) at each trap station. Scented traps were treated by placing approximately 10 grams of scat across the entrance to the trap which emulated a typical encounter by these marsupials with such odours in the wild, and avoided any complications associated with trap dirtiness (Dickman 1992; Banks 1998). Both predator species use scats in scent marking (Macdonald 1979; Kruuk and Jarman 1995; Henry 1996; Burnett 2000); depositing scats in obvious and/or elevated positions along natural thoroughfares such as rocky creek beds or the bases of cliffs, as well as along human thoroughfares, such as roads (Belcher 1995; Kruuk and Jarman 1995; Triggs 1996; Burnett 2000). Thus scats are likely to be encountered by prey species, providing indications of the potential predator activity (Dickman 1992; Banks 1998).

Tiger Quoll scats were collected from captive quolls held at Featherdale Wildlife Park in Sydney fed on a varied diet similar to what they would have in the wild, including poultry, rat, rabbit and macropods. Red Fox scats were collected from captive foxes at the CSIRO Sustainable Ecosystems Unit in Canberra fed on a diet of sheep and kangaroo carcasses and dog food. Scats were either used fresh, or frozen for later use.

Results

Capture success was variable across the four species, though low as typical in studies of such medium-sized mammals. There were eight captures of Southern Brown Bandicoots (2.0%) and 11 captures of Northern Brown Bandicoots from 405 trap-nights (2.7%), and 21 captures of Long-nosed Bandicoots (4.9%), and 13 captures of Common Brushtail Possums from 432 trap-nights (3.0%). Most captures were of adult individuals (mean weight \pm SE), Southern Brown Bandicoots, 699 ± 172 g; Northern Brown Bandicoots 978 ± 124 g; Long-nosed Bandicoots 800 ± 202 g. There were also two recently independent young Northern Brown Bandicoots weighing 160 g and 176 g, both trapped in quoll scented traps. In past studies very few Northern Brown Bandicoots of this size (100-350 g) have been trapped (Hall 1983), and it has been assumed that animals of this size have a very high mortality (Gordon 1974; Hall 1983). Common Brushtail Possum weights were not measured to avoid unnecessary stress on animals, however all were full grown adults.

Chi-squared analysis showed no significant difference among treatments for captures of Long-nosed Bandicoots ($\chi^2_2 = 3.714$, $P = 0.156$) or Southern Brown Bandicoots ($\chi^2_2 = 3.250$, $P = 0.197$). In contrast, there were differences in captures for Northern Brown Bandicoots ($\chi^2_2 = 11.64$, $P = 0.003$) and Common Brushtail Possums ($\chi^2_2 = 8.00$, $P = 0.018$) (Figure 1). But contrary to predictions, captures for both species were higher in quoll-scented traps than in untreated traps (Sign Test, $P < 0.05$). No species showed any response to fox odours.

The inclusion or exclusion of recaptures and captures when another trap at that trap station had been occupied had no effect on the lack of significant difference for Long-nosed Bandicoots and Southern Brown Bandicoots as these captures were spread evenly among the three trap types,

the same as the rest of the captures. One Northern Brown Bandicoot capture was a recapture at a different trap station, but both captures of this animal were in quoll-scented traps. One Northern Brown Bandicoot was captured in a quoll-scented trap at a trap station where an Eastern Chestnut Mouse *Pseudomys gracilicaudatus* had been caught in a fox-scented trap on the same night. The unscented trap at this trap station remained open and unoccupied. Removal of these two captures from the analysis still yielded a significant result ($\chi^2_2 = 8.00$, $P = 0.018$). Two captures of Common Brushtail Possums in quoll-scented traps and the one capture in an unscented trap occurred when the fox-scented trap at that station was occupied by Black Rats *Rattus rattus* for the quoll-scented traps and a Long-nosed Bandicoot for the unscented trap. The other trap at each of these stations remained open and unoccupied. One quoll-scented trap caught a Common Brushtail Possum on two consecutive nights, and this may have been a recapture. The removal of these four captures from the analysis still yielded a significant result ($\chi^2_2 = 6.00$, $P = 0.050$).

Discussion

Neither the bandicoots nor possum showed any avoidance of fox faecal odours. This result contrasts with other studies of prey responses to fox odours where predator and prey have co-evolved (Dickman and Doncaster 1984; Calder and Gorman 1991). However, it concurs with other Australian studies of rodents (Banks 1998) and macropods (Blumstein *et al.* 2002) which similarly showed no responses to fox faecal odours. Yet House Mice in Australia, which have co-evolved with foxes, do avoid fox odours (Dickman 1992; but see Powell and Banks 2004). Together, these results support the notion that foxes are an evolutionarily novel predator, and their odours are not avoided by potential native prey in order to reduce their risks of predation (Banks 1998). Such naiveté may in part explain their particular vulnerability to

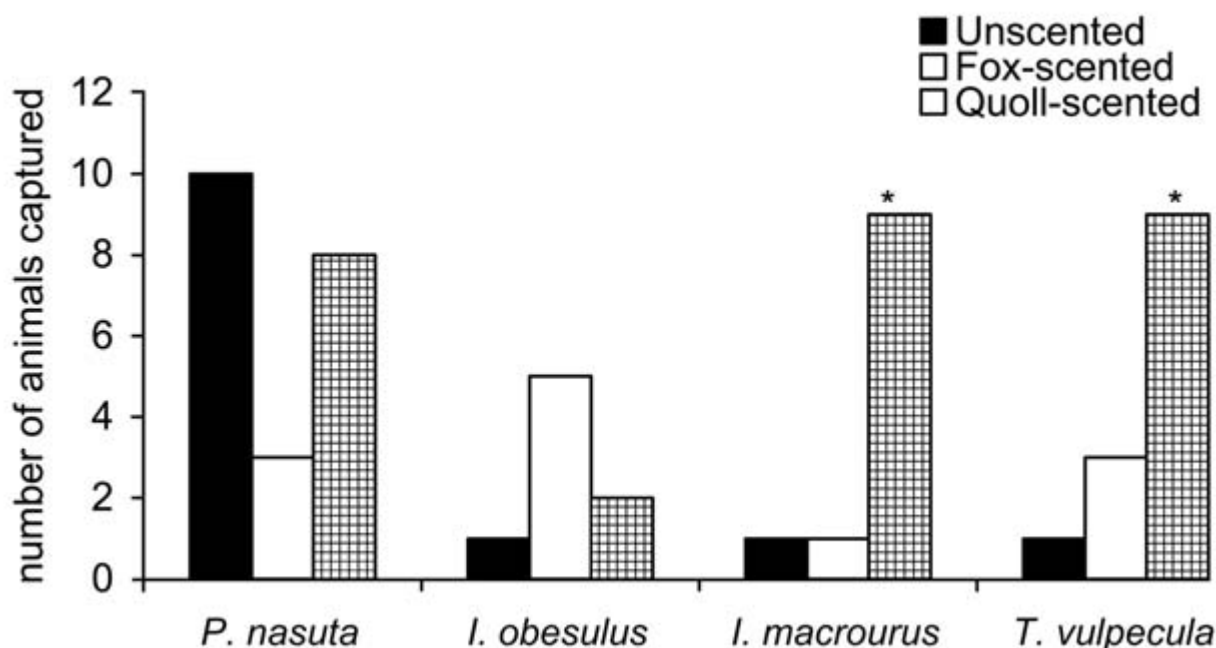


Figure 1. The number of Long-nosed Bandicoots, Southern Brown Bandicoots, Northern Brown Bandicoots and Common Brushtail Possums caught in unscented traps, traps scented with fox faeces, and traps scented with quoll faeces. * represents a significant difference from random entry of traps at the $P = 0.05$ level.

foxes. However, these animals may use other behavioural means to reduce their likelihood of predation. For example, Gresser (1996) found that Common Brushtail Possums ate fewer pieces of apple and sultana from areas tainted with Red Fox urine and faeces than untainted areas, so although they were not avoiding the area entirely, they were presumably spending less time there.

Similarly, none of these CWR marsupial species showed avoidance of native Tiger Quoll odours. Instead, Northern Brown Bandicoots and Common Brushtail Possums both appear to be attracted to the odour of the Tiger Quoll. Tiger Quolls use scats in scent marking, often defecating in communal latrines (Kruuk and Jarman 1995). Latrine sites would represent particularly dangerous places, with frequent visitation by quolls. Kruuk and Jarman (1995) recorded scat deposition rates of 1.35 to 1.9 scats per latrine per day, increasing to 3.4 scats per day when food was abundant. Claridge *et al.* (2004) noted that quolls do not always deposit scats when visiting latrines. The presence of quolls at the latrine several times per day would presumably lead to a higher risk of predation from the latrine user and other quolls attracted to the odours. Hence it appears that these two species may be at higher risk of predation if they are attracted to quoll faecal odours.

Quoll scats may represent a possible source of invertebrates for bandicoots and possums. Dickman and Doncaster (1984) found that Common Shrews *Sorexorex* did not avoid Red Fox scats, and suggested that scats may attract certain beetles, which the insectivorous shrews would prey upon to outweigh predation risks from foxes associated with fox scats. Bandicoots, while omnivorous, prefer to eat insects and other invertebrates (Quin 1988; Gott 1996; Scott *et al.* 1999) some of which may be associated with scats, and Common Brushtail Possums are also known to consume invertebrates when readily available (Kerle 2001), but are otherwise largely herbivorous. Quoll scats may therefore be a highly profitable resource rich patch to be exploited by both species, whereas the similar value of fox scats may not be recognised because they are recent arrivals to Australia. However, it is not clear why this would be the case for the Northern Brown Bandicoot and the far less insectivorous Common Brushtail Possum, and not for the more insectivorous Long-nosed and Southern Brown Bandicoots.

It is also possible that bandicoots and possums showed an anti-predator response in spite of the apparent attraction to traps with odours. In response to a perceived predation threat that may be imminent, prey can either opt for flight or concealment. Some rodents exposed to predators take flight and flee while others may freeze (Jedrzejewski *et al.* 1992). But both in the wild and in the lab, imminent predator threat causes many animals to take refuge in the nearest

refugium, typically somewhere where predators cannot follow (Jedrzejewski *et al.* 1992; Dielenberg *et al.* 1999). It may be that these species respond to predator odours, by entering the nearest appropriately sized hole, which in this case is a trap. Both Northern Brown Bandicoots and Common Brushtail Possums nest in natural hollows (Gordon 1998; Kerle 2001) and take shelter when approached.

But why do Long-nosed and Southern Brown Bandicoots not respond to quoll odour in the same way as Northern Brown Bandicoots and Common Brushtail Possums? One possible reason is size-dependent risks of predation from quolls influencing prey responses to odours. Common Brushtail Possums may weigh more than 4 kg, and Northern Brown Bandicoots may weigh more than 3 kg, whereas both the Southern Brown Bandicoot and Long-nosed Bandicoot seldom weigh more than 1 kg (Strahan 1998). As such these smaller species are likely to have been vulnerable to predation by Eastern Quolls *D. viverrinus* before this native predator became extinct on the mainland, as Eastern Quolls are thought to prey on animals up to a size of 1.5 kg (Jones and Rose 2001), whereas the larger prey would only be at risk from Tiger Quolls. Small prey would therefore be expected to strongly avoid areas with odours from any quoll species while larger prey should show more species specific responses to predator odours (Jedrzejewski *et al.* 1993) to avoid costs of unnecessary odour avoidance. In support of this concept we found that even allowing for a single trap at each trap station, trap success for Long-nosed Bandicoots was lower than the long term average success for the population (14.6% vs 22%) (NPWS, unpublished data) suggesting some avoidance of the trap stations as opposed to finer scale odour discrimination. In contrast, the apparent attraction of larger prey species to quoll odours may represent a strategy of odour inspection to discriminate amongst odour donors, information which is often found in the less volatile components (Nevison *et al.* 2003) requiring closer contact. But once the predation risk was identified, the larger prey took refuge. To test this hypothesis further, finer scale information is needed about the immediate behavioural responses to predator odours by these prey species.

None of these four CWR species avoided the odour of the introduced Red Fox. Such apparent naiveté to fox odour cues may put them at higher risks of predation than introduced species which do avoid fox odours, and may in part explain their particular vulnerability to fox predation. However, they may respond in other ways which do not affect their trappability. Common Brushtail Possums and Northern Brown Bandicoots appear sensitive to odours from native Tiger Quolls, but they may be adopting a strategy of predator inspection. Future work on these odour-mediated predator prey interactions will benefit from resolving the fine scale behavioural responses of prey to different odour sources.

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